Brock University

HABITAT SELECTION OF THREE RODENTS IN A FREQUENTLY BURNED BOREAL ENVIRONMENT: PRODUCTIVITY AND HABITAT DIVERSITY

by

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A Thesis

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ABSTRACT

Productivity and habitat diversity in relation to the habitat selection of three microtine rodents, Microtus pennsylvanicus, Microtus xanthognathus, and Clethrionomys rutilus in a frequently burned northern boreal environment.

by

Donald John Mc Donald

How does fire affect the plant and animal community of the boreal forest? This study attempted to examine the changes in plant composition and productivity, and small mammal demography brought about by fire in the northern boreal environment at Chick Lake, N.W.T. (65°53'N, 128°14'W).

Two 5.6 ha plots measuring 375m x 150m were selected for study during the summers of 1973 and 1974. One had been unburned for 120 years, the other was part of a fire which burned in the spring of 1969. Grids of 15m x 15m were established in each plot and meter square quadrats taken at each of the 250 grid intersections in order to determine plant composition and density. Aerial primary production was assessed by clipping and drying 80 samples of terminal new production

for each species under investigation. Small mammal populations were sampled by placing a Sherman live trap at each grid intersection for ten days in every month.

The two plots were similar in plant species composition which suggested that most regrowth in the burned area was from rootstocks which survived the fire. The plant data were submitted to a cluster analysis that revealed nine separate species associations, six of which occured in the burned area and eight of which occured in the control. These were subsequently treated as habitats for purposes of comparison with small mammal distributions. The burned area showed a greater productivity in flowers and fruits although total productivity in the control area was higher due to a large contribution from the non-vascular component. Maximum aerial productivity as dry wieght was measured at 157.1 g/m^2 and 207.8 g/m^2 for the burn and control respectively. Microtus pennsylvanicus and Clethrionomys rutilus were the two most common small mammals encountered. Microtus xanthognathus, Synaptomys borealis, and Phenacomys intermedius also occured in the area. Populations of M. pennsylvanicus and C. rutilus were high during the summer of 1973; however, M. pennsylvanicus was rare on the control but abundant on the burn, while C. rutilus was rare on the burn but abundant in the control. During the summer of 1974 populations declined, with the result that few voles of any species were caught in the burn

while equal numbers of the two species were caught in the control.

During the summer of 1973 M. pennsylvanicus showed a positive association to the most productive habitat type in the burn which was avoided by C. rutilus. In the control C. rutilus showed a similar positive association to the most productive habitat type which was avoided by M. pennsylvanicus. In all cases for the high population year of 1973, the two species never overlapped in habitat preference. When populations declined in 1974, both species showed a strong association for the most productive habitat in the control. This would suggest that during a high population year, an abundant species can exclude competitors from a chosen habitat, but that this dominance decreases as population levels decrease. It is possible that M. pennsylvanicus is a more efficient competitor in a recently burned environment, while C. rutilus assumes this role once non-vascular regrowth becomes extensive.

ACKNOWLEDGEMENTS

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INTRODUCTION

Fire in forested areas has traditionally been viewed as a destructive element in the environment. Recent studies indicate that fire is actually an important part of ecosystem development, especially in boreal regions. Heinselman (1971,1973) outlined the role of fire in maintaining floral diversity of forested areas in Minnesota. Rowe and Scotter (1973) and Kershaw (1976) documented the long history of fire in the borel forests of Canada, and its importance in creating and maintaining a diverse natural landscape. These authors state that without the presence of fire in the boreal zone, long term successional change would lead to the climax of a few coniferous dominants and the decline of many floral communities which are fire dependent. Viereck (1973) notes that much of the boreal region is thus maintained in what is a relatively early successional state, and Selleck (1960) criticized the use of the term climax in such a situation.

Some authors feel that one immediate effect of fire is increased productivity of pioneering species due to an increase in nutrients released to the soil (Ahlgren and Ahlgren 1960, Old 1969, Viro 1974). This may be of great importance in boreal areas located on permafrost. Rowe and Scotter (1973) outlined the importance of deep thawing after a burn in releasing previously frozen ground to exploration by plant

roots. Viereck (1973) noted in Alaska that the blackened surface of a fresh burn and lack of insulating ground cover produced an increase in soil temperature and thaw depth due to absorption of solar energy.

Direct evidence of nutrient benefits after fire is given by Wien and Bliss (1973) and Wien (1974) who found that burned Eriophorum tussocks recovered rapidly with an increased nutrient content of individual plants. Janz (1973) and Weber (1974) found that the soil nutrient pool of a boreal community located on permafrost showed a net increase after fire, although Viro (1974) noted that some nutrients, potassium and phosphorous in particular, are rapidly leached to a depth beyond the reach of early colonizing plant species.

Animal populations are intimately associated with floral communities and are thus affected by fire-induced changes (Shelford and Olson 1935). Fire is initially destructive to caribou (Rangifer tarandus) habitat; however, open lichen woodland which forms the winter range for this deer would disappear beneath an encroaching moss mat if it was not regularly renewed by fire (Kershaw 1976). Small mammals are usually able to survive the initial effects of a burn and must then disperse to unburned "islands" or more distant unburned habitat (Cook 1959). As succession proceeds in the burned area, new plant communities develop and pioneer-

ing animal species begin to return.

The study attempted to examine a boreal situation at this point by studying the plant communities, productivity, and rodent populations of a recently burned area in comparison to an "old burn" control. Small mammals tend to be somewhat habitat-specific (Whitney 1976, Iverson and Turner 1972) and are thus good indicators of habitat development after a disturbance (LoBue and Darnell 1959). Northern boreal areas on permafrost are interesting since many species such as the jackpine (Pinus banksiana) which normally succeed a fire in southern boreal regions are missing (Zoltai and Pettapiece 1973). Small mammal demography in far northern areas is also of interest since many species such as the meadow vole (Microtus pennsylvanicus) are found over a wide range.

Northern environments have been described as "fragile" (Reid 1974) and this raises concern over the increasing activity of man with the resulting risk of greater fire frequency. Dunbar (1973) questioned this assumption and stated that arctic ecosystems are no more sensitive to disturbance than any other. Fire is a common disturbance in northern boreal areas and as such presents the opportunity to study the response of plant and animal communities to a form of disturbance which may become increasingly prevalent in future.

STUDY AREA

The project was carried out at Chick Lake, N.W.T. (65 53'N, 128 14'W), approximately 100 km northeast of Norman Wells (Fig. 1) during the summers of 1973 and 1974. The lake is situated in a broad valley between two limestone ridges. The lakeshore rises gently on all sides to eventually meet these ridges, but is otherwise level. The control grid was established at the northwest end of the lake and aged by fire scars as having been unburned for a hundred and twenty years. The burn plot was established in an area at the west end of the lake which burned in 1969. Reid (1974) gives the average fire frequency in this area as being between 120 to 150 years on the basis of fire scars and soil carbon layers.

The control area was heavily forested by black spruce (Picea mariana) with some paper birch (Betula papyrifera) and carpeted with a thick layer of moss and lichens (Fig. 2). The burned area lacked trees and supported few non-vascular species, although understory growth was returning rapidly (Fig. 3). One old seismic line and one recent cutline transect the burned area. The cutline had been used as a winter road prior to 1973, but was abandoned in the winter of 1973-

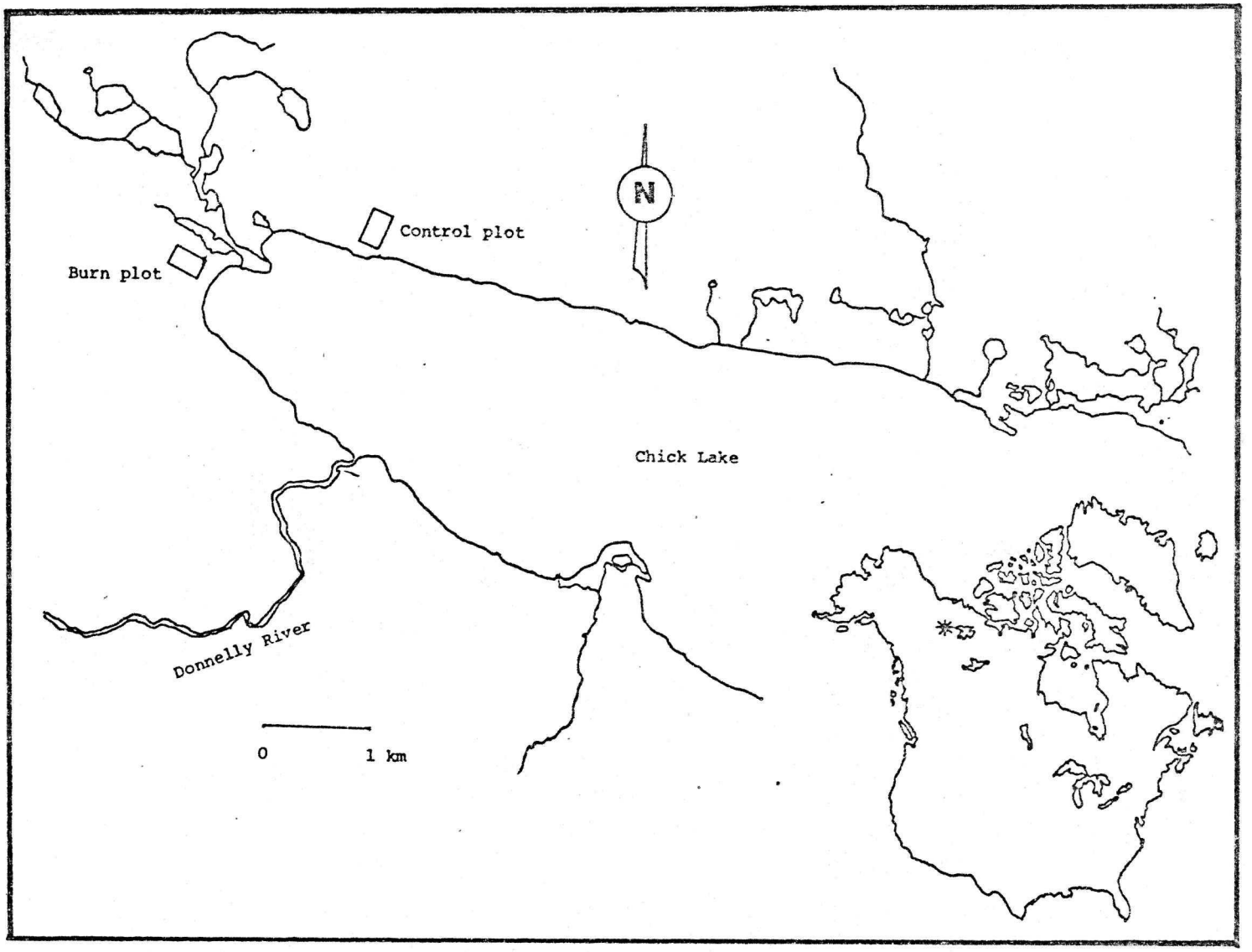
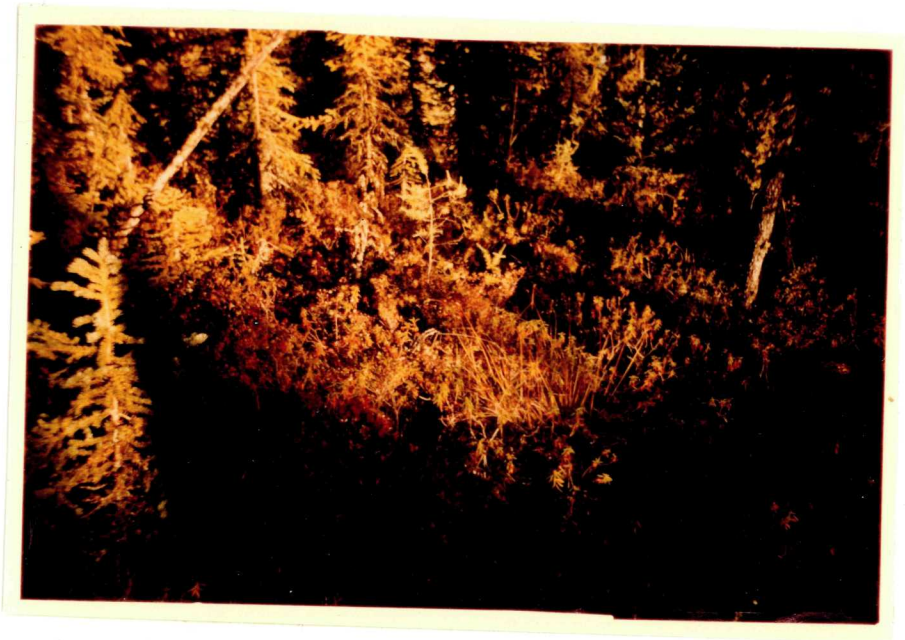


Fig. 1. Location of Chick Lake study area.
* area of study

a.



b.

Fig.2. a. Control grid from the air. b. Ground cover on grid.

a.

b.

Fig.3. a. Burn grid from the air. b. Ground cover on grid.

74. During the 1974 summer field season another small cut-line was cleared through the area as the initial stages in construction of the proposed Mackenzie Highway.

MATERIALS AND METHODS

COLLECTION OF PLANT DATA

Two plots 5.6 ha in area were established, one in the old burn control and one in the 1969 burn. These were known as the control plot and burn plot, respectively. Grids of 15 m x 15 m were layed out within each plot. Grid spacing was chosen to facilitate small mammal trapping as this is the standard grid size chosen for IBP work (Pelikan 1967). Hulten (1968) was used as the key for all plant identification. All Gramineae, Carex and Salix species were sent to the Herbarium of the University of Saskatchewan at Saskatoon for confirmation of identification.

Meter square quadrats were taken at each of the 250 grid intersections in each plot. Plant species occurring within the quadrat were recorded, including any individuals which extended into the quadrat but were rooted outside of its boundaries. Cover of each species was estimated as either 5% or to the nearest 10% of the square meter. In order to facilitate cover estimations, the quadrat was divided in half, and one half divided in half again. This resulted in

one 50% area and two 25% areas. One 25% area was then divided into a 10-cm grid with fine wire so that each subdivision represented 1% of one square meter. Originally the entire quadrat was subdivided into a 10-cm grid; however, this proved unworkable since it was difficult to place the quadrat if small shrubs were present. Such precise cover estimates were necessary in order to facilitate productivity assessments. Thaw depth was taken with a metal probe and measured from the ground surface (moss surface in the control) to the first ice layers encountered.

PRIMARY PRODUCTIVITY

NET AERIAL PRIMARY PRODUCTIVITY IN VASCULAR SPECIES

Terrestrial primary productivity assessments have traditionally entailed clipping a quadrat of vegetation, recording the dry weight and expressing this measurement in terms of a unit area (Macfadyen 1948, Westlake 1963). This is best carried out in uniform plant communities having a high density of individuals such as grasslands. The highly heterogenous ground flora found in a boreal situation does not lend itself to such analysis, and the method used in this study follows that developed by Reader and Stewart (1971) for use in measuring the primary production of bog vegetation in southwestern Manitoba.

The maximum dry weight production in all plant species could be measured at the end of the growing season in the fall when production of new tissue stopped. Such a single measurement would however underestimate total productivity sinceshort lived structures such as flowers and fruits which are produced and lost during the growing season would not be measured.

A single fall measurement would not permit a comparison of the progress of growth over the summer. Information such as the date and extent of flowering or fruit production of a species compared between the two areas would be lost. In order to overcome this problem, the two plots were sampled every two weeks during the 1974 field season. This allowed the phenology of production in each area to be monitered as growth proceeded over the course of the summer. Maximum dry weights recorded for the various short term structures were added to maximum vegetative dry weight production found at the end of the growing season in order to produce a total productivity value for each species.

The technique developed by Reader and Stewart (1971) requires the definition of growing points for each species sampled. A growing point is the location of new tissue production on a plant and includes new stem and leaf, flowers, fruits, and radial increment of existing stems. Perennial

leaves from the previous year are not included in productivity measurements since Reader and Stewart (1972) have shown that no weight gain takes place in perennial components after the first growing season.

Growing points were identified for each species under consideration. These points of new tissue production were considered to be new leaf, new stem, flowers or fruits. Thus at every bi-weekly sampling day, these structures were clipped and weighed for the species of interest in each plot. Experimentation revealed that 80 samples of each growing point for a given species were necessary at every sampling date in order to obtain a standard error of less than 10%. These samples were clipped randomly throughout both plots and dried for 24 hours in a propane fired drying oven. The total dry weight for each group of growing points was recorded on a torsion balance, and the ratio total weight/80 gave the mean dry weight per growing point.

In order to express this value on a per meter basis the density of the various growing points was assessed by throwing meter square quadrats randomly. The cover of each plant species in the quadrat was recorded, and the number of growing points for each species was counted. Thus species A might have a cover value of 15%m^2, and display 20 new leaves, and 10 flowers within that 15%m^2. In order to facilitate

further calculations these growing points were expressed per unit area of one m^2. For example. if 0.15 m^2 of species A produced 20 leaves and 10 flowers, one m^2 would produce 1.0/0.15 x 20= 133.3 leaves /m^2, and 1.0/0.15 x 10= 66.7 flowers/m^2. Experimentation revealed that 20 such quadrats were necessary for each species in order to obtain a standard error for growing point density of less than 10%.

As outlined previously, the weight of individual growing points was known at each sampling date, and multiplying this weight by the density obtained above gave the dry weight production/m^2 for each class of growing points, or new leaves and flowers in the case of species A. Combining the production of these components gave the total production for species A. For example, suppose on the August 17 sampling date, the mean weight for leaves was 2 g/leaf and that for flowers was 0.5 g/flower. Total productivity for species A would have been:

(133.3 leaves/m^2 x 2 g/leaf) + (66.7 flowers/m^2 x 0.5 g/flower)

or 299.9 g/m^2. This assumes that the entire quadrat is filled with species A, as would be the case if the plot was located in a grassland and each quadrat taken was filled with one species. Such is not the case in a boreal situation however, and the above value for total production must be corrected by multiplying it by the actual mean cover

value found for the species. Thus, if the mean cover of species A was found to be 12.5%m^2 in the initial quadrat survey of the plot, the actual total productivity for the species on August 17 would have been 299.9g/m^2 x 0.125 = 37.5g/m^2. Those species which also retained perennial parts from previous growing seasons were clipped and weighed in order to make an assessment of total standing biomass in the two plots.

Only those species with a relative frequency of occurrence greater than or equal to 5% were considered for direct productivity measurements, as those which fell below this point would not occur frequently enough to make an important contribution to the production of the area. The productivity of the less important species was estimated by comparing their weights of new growth with those of the more important species and calculating the percentage contributed by the less important species. The aerial production totals were then increased by this amount. These totals were also increased in order to account for secretion and consumption losses. No direct measurement of these losses was made, however Reader and Stewart (1971) estimated from their own work and that available in the literature a correction factor of 6% of the total measured productivity. The values obtained in this study were increased by that amount in order to avoid underestimating total production.

In order to measure the annual radial increment of shrubs and willows, ten stems were selected randomly for each woody species. These were then aged by growth rings, dried for 24 hours and weighed. The average weight increment per year was then used to calculate current woody production. No attempt was made to measure primary production of mature tree species on the control since such measurements would have little relationship to comparisons with the burn.

NET AERIAL PRIMARY PRODUCTIVITY IN NON-VASCULAR SPECIES

Growing points in Aulacomnium nitens were identified by the presence of chlorophyll in individual plants (Reader and Stewart 1971). These were then clipped, dried, and weighed. Twenty plugs of moss, 5cm x 5cm were counted to obtain the mean density of growing points per square centimeter. This was then multiplied by the mean cover value in square centimeters per square meter. The result, when multiplied by the average dry weight per growing point gave the net non-vascular primary productivity. For example, if species B had a density of 10 growing points (g.p.)/cm^2, a mean cover of 20% ($0.2m^2$), and a mean dry weight of 0.3 g/g.p., net primary productivity for the species would be given by;

$$10 \text{ g.p.}/cm^2 \times 2000 \ cm^2/m^2 \times 0.3 \text{ g/g.p.} = 6000 \text{ g}/m^2$$

In order to correct for those species below a relative

frequency of 5%, the following ratio was calculated:

$$\frac{\text{sum of cover values for less important species}}{\text{sum of cover values of important species}} \times 100\%$$

Measured non-vascular net primary production was then increased by this amount.

SMALL MAMMALS

SMALL MAMMAL TRAPPING

In order to assess the small mammal populations in the plots, live trapping was carried out during the summers of 1973 and 1974. One Sherman live trap was placed at each grid intersection in both plots. The traps were filled as much as possible with terelyne nest material in order to reduce mortality from hypothermia and baited with a mixture of rolled oats and commercial laboratory rodent feed which had been waterproofed with vegetable oil. Terelyne was found to provide much better insulation than cotton under wet conditions. In order to standardize my work with that being carried out in this and other areas of the proposed pipeline route, I used the 10 day small mammal trapping period adopted by the various consulting services involved in the biological survey of the route. The control grid traps were opened for the first ten days of each month, and the burn grid traps were opened for the second ten days of each month.

Traps were run in the morning and again in the evening, and always left in place in the grids even when closed. The two grids could not be run simultaneously because of their isolation from each other and the difficulty in obtaining access to the control grid.

When an animal was caught, the trap location, species, sex and weight were recorded. The animal was then toe-clipped for identification and released at the point of capture. Population size was measured by enumeration, or known trappable population (KTP). Hillborn et al. (1976) have shown this method to produce results which compare favorably with the Jolly(1965) method, although enumeration consistently underestimates the actual population size by 10 to 20%.

HABITAT ASSESSMENT

The term "habitat" is subject to definition according to the parameters which are used in its measurement. Pielou (1969) speaks of "habitable units" which may or may not be discrete. The concept of habitat and niche often overlap and may merge into one as the breadth of information defining a habitat increases (Pielou 1972). In the case of small mammals the immediate floral environment can be considered as a central component in the animals' habitat (Douglass 1976). M'Closky (1976) and M'Closky and Fieldwick (1975) have also

considered physical characteristics of the environment which may limit an animals ability to move, reproduce, and find suitable nesting areas.

The question of what actually constitutes a habitat cannot be resolved fully until all the environmental requirements for a given animal are known. We may assume that the spatial distribution of an animal will include that portion of the environment for which it is most fit. We may also assume that the "choicest" part of that portion will be that area in which the animal spends the majority of its time, or in which it is encountered most frequently. The nature of the environment is important since Grant and Morris (1971) predict that animal populations will become more aggregated as the habitat becomes more patchy. The forest floor of a boreal area may be considered extremely patchy, as few vascular species grow in uniform stands. This is especially true of the burn plot which lacks a deep moss and lichen cover.

In this study it was assumed that a definable habitat would be similar throughout its spatial domain and thus discrete blocks of the two plots were grouped according to their similarity. The parameters used for this purpose were cover of all plant species measured by quadrat analysis at each trapping site, depth of vegetation, and net primary

productivity of each trapping location. Depth of vegetation was taken from the highest component in the quadrat to mineral soil in the burn, and the surface of the moss layer in the control. Moss layer depth in the control was considered to extend from the surface of the mat to permafrost.

Agglomerative analysis has been used successfully in environmental classification (Orloci 1967, Ohman and Ream 1971) and was chosen for this study. The data from the habitat measurements were submitted to analysis using a cluster program developed by Wishart (1975) and the results displayed as a spatial grouping of the most similar trapping locations in both grids. Small mammal distributions were then tested against these groupings using X^2 to determine any associations with these groups in the two different areas (burn and control) and the two different population sizes (1973 and 1974).

RESULTS

RESULTS OF QUADRAT ANALYSIS

The burn contains three species which are not represented on the control, while the control contains six species, mostly cryptogams, not seen on the burn (Table 1). A simple Jaccards co-efficient, species in common/total number of species x 100% (Grieg-Smith 1964), yielded a similarity value of 76%. Most regrowth in the burn took place from rootstocks which survived the fire rather than originating from wind-blown seed. Average thaw depth on the burn was 80 cm; that on the control was 20 cm.

PRIMARY PRODUCTIVITY ASSESSMENT

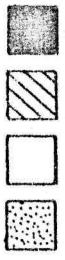
Growth in both areas was rapid in June (Fig. 4), after which dry weight values fluctuate. Maximum dry weight was obtained in August for both areas. Primary productivity analysis was carried out on those species listed in Table 1 above or equal to a 5% frequency value with the exception of Equisetum scirpoides and Polytrichum juniperinum on the burn, and Cladonia rangiferina on the control. It was not possible

TABLE 1

Relative frequency and cover values of species found in the study areas

Burn species	% frequency occurrence	Cover %m^2	Control species	% frequency occurrence	Cover %m^2
Vaccinium uliginosum	13.5	12.6	*Vaccinium uliginosum*	11.1	12.6
Ledum groenlandicum	11.0	7.5	*Vaccinium vitis-idaea*	10.5	8.7
Carex lugens	9.7	20.0	*Arctostaphylos rubra*	9.9	8.9
Salix arbusculoides	7.5	9.7	*Ledum groenlandicum*	8.6	8.9
Arctostaphylos rubra	7.2	9.1	*Aulacomium nitens*	8.3	17.5
Vaccinium vitis-idaea	6.2	6.0	*Carex lugens*	7.2	10.2
Equisetum scirpoides	5.5	6.9	*Cladonia rangiferina*	5.7	12.2
Polytrichum juniperinum	5.5	9.6	*Salix arbusculoides*	5.2	7.9
Calamogrostis canadensis	4.5	12.0	*Rosa acicularis*	4.9	5.1
Potentilla fruticosa	4.3	5.9	*Hylacomium splendens*	4.8	16.3
Rosa acicularis	4.2	6.2	*Equisetum scirpoides*	4.7	6.7
Picea mariana	3.2	5.2	*Polytrichum juniperinum*	3.3	8.0
Epilobium angustifolium	2.3	5.8	*Alnus crispa*	2.7	11.5
Alnus crispa	1.9	18.3	*Empetrum nigrum*	2.3	7.3
Betula glandulosa	1.9	11.3	*Betula glandulosa*	1.7	7.6
Pyrola grandiflora	1.7	5.1	*Pyrola grandiflora*	1.7	5.3
Rubus chamaemorus	1.7	5.0	*Tomenhypnum nitens*	1.7	12.6
Salix glauca	1.5	11.4	*Potentilla fruticosa*	1.5	5.5
Ledum palustre	1.3	8.3	*Pyrola secunda*	1.4	5.0
Eriophorum spissum	1.2	10.4	*Calamogrostis canadensis*	0.8	5.0
Tomenhypnum nitens	1.1	15.0	*Picea mariana*	0.4	7.5
Ribes triste	1.0	17.5	*Rubus chamaemorus*	0.4	5.0
Pyrola secunda	0.6	5.0	*Ledum palustre*	0.3	7.0
Equisetum arvense	0.4	5.0	*Salix glauca*	0.3	11.3
Aulacomium nitens	0.3	6.7	*Shepherdia canadensis*	0.3	5.0
Betula paperifera	0.3	5.5	*Ribes triste*	0.2	5.0
Chamaedaphne calyculata	0.09	5.0	*Cetraria sp.*	0.2	6.7
Viburnum edule	0.09	10.0	*Betula paperifera*	0.06	5.0
Shepherdia canadensis	0.09	5.0	*Eriophorum spissum*	0.06	5.0
Sphagnum sp.	0.09	12.5	*Sphagnum sp.*	0.06	10.0
Larex laricina	0.09	5.0	*Orchus rotundifolia*	0.06	5.0
			Larix laricina	0.06	5.0
			Chamaedaphne calyculata	0.06	5.0
			Peltigera sp.	0.06	5.0

Fig. 4 . Phenology graph for the 1974 growing season

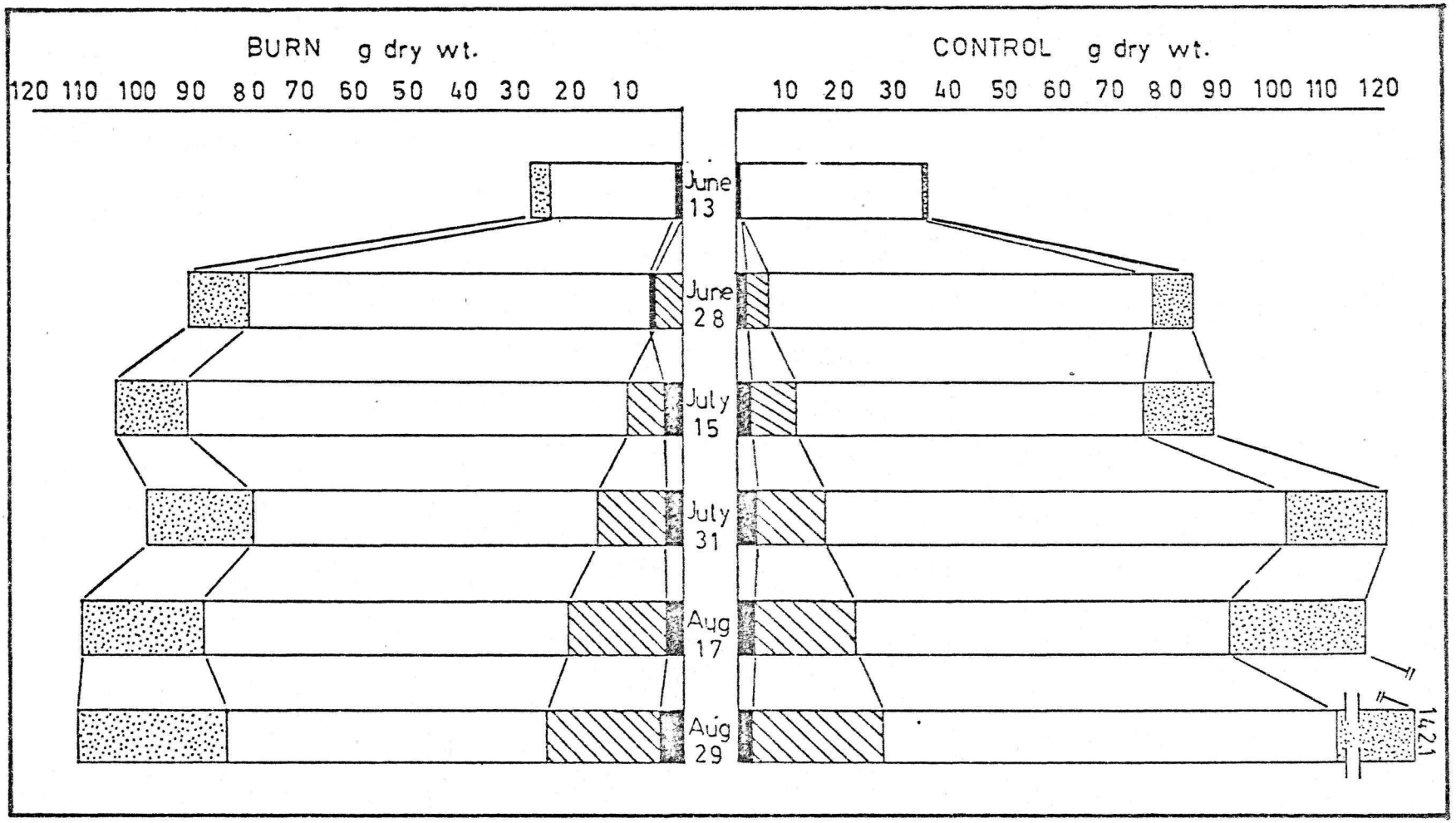


flower-fruit

radial increment

new leaf

total dry weight productivity


BURN g dry wt.
120 110 100 90 80 70 60 50 40 30 20 10
CONTROL g dry wt.
10 20 30 40 50 60 70 80 90 100 110 120
June 13
June 28
July 15
July 31
Aug 17
Aug 29
142.1

to distinguish new growth in these species and their yearly productivity is extrememy low (Hale 1967, Reader and Stewart 1971). Maximum net primary productivity values are given in Tables 2 and 3 for the burn and control plots, respectively. The results of the quadrat analysis in Table 1 revealed that the same vascular species occur above the 5% frequency value in both plots, a further indication of the similarity in ground flora between the two areas.

Production values for all vascular species with the exception of Vaccinium vitis-idaea and Ledum groenlandicum were higher in the burn plot. L. groenlandicum, however, had a higher production of flowers and fruits in the burn. Both Salix arbusculoides and Vaccinium uliginosum show an increase in density of rooted stems in the burn as well as higher productivity values for all components. Non-vascular production in the control accounts for the greatest difference between the plots. Aulacomnium nitens recorded the highest production value of any individual species. The control plot gave the highest value in perennial components, as would be expected due to the longer growing history of perennial plants. In five years, however, the burn had accumulated half the perennial value recorded for the control.

TABLE 2

Burn plot: net primary production of aerial plant components

Species	R/m^2	New leaf Gp/m^2	Flower fruit Gp/m^2	Radial stem increment	Total net aerial production (A)	(C)	Net aerial production all species $\Sigma(A)(C)$	Perennial leaf and stem (D)
		Aerial component production						
Arctostaphylos rubra		17.60 1271.3±6.6	3.20 193.6±49.0		20.8			
Carex lugens		45.40 1709.1±12.0	0.70 122.3±33.0		46.1			
Ledum groenlandicum	345.0±33.4	5.10 975.4±18.0	2.00 527.8±11.2	14.8	21.9			
Salix arbusculoides	4.7±4.0	0.04 3.6±17.0	0.05 9.1±20.0	3.1	3.2	1.086	157.1	77.1
Vaccinium uliginosum	1047.8±21.4	24.20 7379.5±30.6	2.10 360.9±30.4	7.9	34.1			
Vaccinium vitis-idaea		18.50 3538.8±10.6			18.6			
Total measured standing biomass = 234.2								

NOTE: all weights expressed in grams per square meter
R/m^2 = number of rooted stems per square meter ± one standard error as a percentage
Gp/m^2 = number of growing points per square meter ± one standard error as a percentage
C = correction factor for less important species, consumption, and secretion

TABLE 3

Control plot: net primary production of aerial plant components

Species	R/m^2	New leaf	Gp/m^2	Flower fruit	Gp/m^2	Radial stem increment	Total net aerial production (A)	(C)	Net aerial production all species Σ(A)(C)	Total Σ(A)(C)	Perennial leaf and stem (D)
		Aerial component production									
Vascular:											
Arctostaphylos rubra		12.60	888.3±10.2	0.80	172.4±37.0		13.40				
Carex lugens		36.10	1782.3±19.0	0.80	185.3±42.0		37.00				
Ledum groenlandicum	447.7±19.0	6.80	800.0±13.1	0.60	106.7±28.3	21.9	29.20	1.086	134.9..		141.5
Salix arbusculoides	1.3±4.0	0.01	1.2±16.4	0.01	2.5±20.0	0.3	0.04				
Vaccinium uliginosum	226.7±19.4	12.80	4626.6±9.7	1.70	339.3±58.1	5.7	20.20				
Vaccinium vitis-idaea		24.40	2768.6±12.3				24.40			...207.8	
Non-vascular:											
Aulacomium nitens		58.30	16.7±11.0*				58.30	1.250	72.9..		

Total measured standing biomass = 349.3

*Gp/cm^2

NOTE: see Table 2 for explanation of nomenclature

SMALL MAMMAL POPULATIONS

The small mammals encountered in this area during the course of the study included Clethrionomys rutilus, Microtus pennsylvanicus and Microtus xanthognathus. C. rutilus, and M. pennsylvanicus occur widely in the Mackenzie Valley region (Banfield 1974, Fuller 1969); however, M. xanthognathus has a much more restricted range (Lensink 1954). Two Synaptomys borealis were live trapped on the burn, and one Phenacomys intermedius was live trapped in a trapline placed 5 km northwest of the burn grid. P. intermedius has not been previously reported from this latitude (Banfield 1974), and the capture of this individual represents a northern record for the species (Douglass and McDonald 1976). Several specimens of Sorex cinereus were live trapped in a trapline placed in a grassy margin of Chick Lake. All of these were dead upon retrieval.

Known trappable population (KTP) values are given for both areas in Fig. 5. Both M. pennsylvanicus and C. rutilus were at high population levels in 1973, but these peaks occurred separately in the burn and control, respectively. M. pennsylvanicus was declining in population while C. rutilus was increasing. The C. rutilus population reached its highest value in September, after which it declined (Douglass, pers comm). There was a small population of

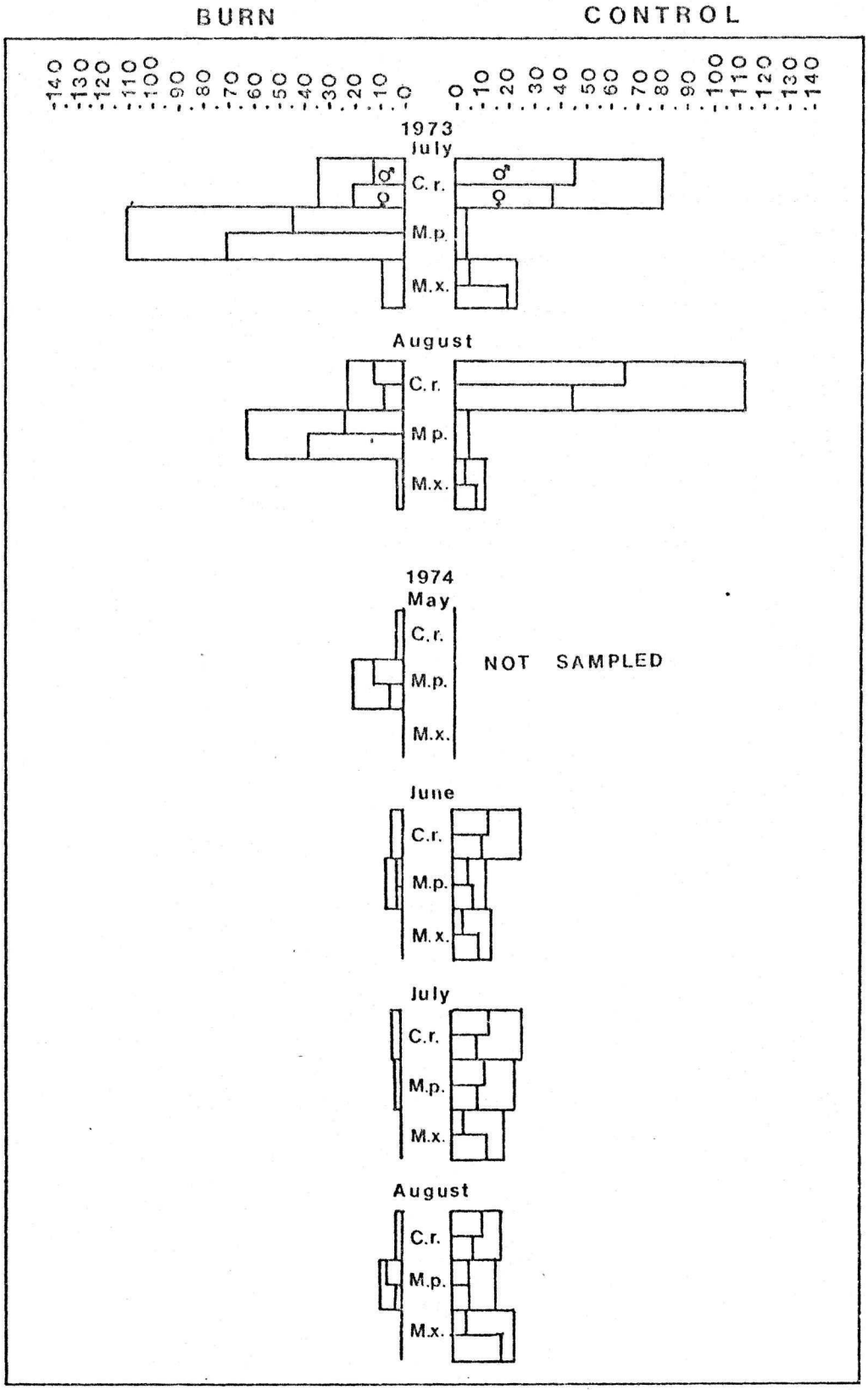


Fig. 5. Known trappable population values in the burn and control for 1973 and 1974.

M. pennsylvanicus still present in the burn in May 1974, but this declined to less than ten individuals for the remainder of the summer. The control was not sampled in May 1974 since ice conditions on the lake did not allow access to the plot. C. rutilus and M.pennsylvanicus remained at roughly equal numbers in the control for 1974.

Male C. rutilus were captured more frequently than females in the control for both years. In July 1973, however, more female C. rutilus were captured on the burn than males. This was the only such instance recorded in the study. The opposite was found for M. pennsylvanicus in the burn in 1973. In 1974, however, the overwintered population in the burn consisted mostly of males. M. xanthognathus essentially disappeared from the burn in 1974, but the population remained relatively stable in the control over both years. More males than females were captured in all cases in the control.

HABITAT ASSOCIATIONS

The clustering program acted essentially as a sorting device. Initially each trapping site in the burn and control was assigned to one of 15 initial clusters. The cover values for each site were compared to the mean cover values for each of the 15 initial clusters. If a trapping site proved to be more similar to a cluster other than the one in which it was initially situated, it was moved to that cluster. This re-

location cycle continued until no further changes occurred at which point the two most similar clusters were fused and the relocation cycle began again for the 14 cluster level. This process continued until 2 terminal clusters had been reached. In order to check the results of the analysis, three different starting arrays, or random starts were used, and the results of the similarity groupings compared at each cluster level.

Similarity within each cluster was assessed by computing an F value of within cluster variance compared to total variance for each parameter, given by;

$$\frac{s^2_{xj}}{s^2_{xtotal}}$$

where x is the parameter, and j is the cluster. A minimum F value corresponds to a minimum within cluster variance, and thus identifies the cluster level in which the groups are most similar. These values are graphed in Fig. 6. The first and third random starts showed minima at the 10 cluster level. The second random start showed a minimum at the beginning of the run and again at the 9 cluster level. Examination at the 10 cluster level revealed two indistinguishable clusters which were fused at the 9 cluster level. These nine clusters were separate and distinct, and this level was chosen as representative of the floral associations in the two plots. The components of these clusters

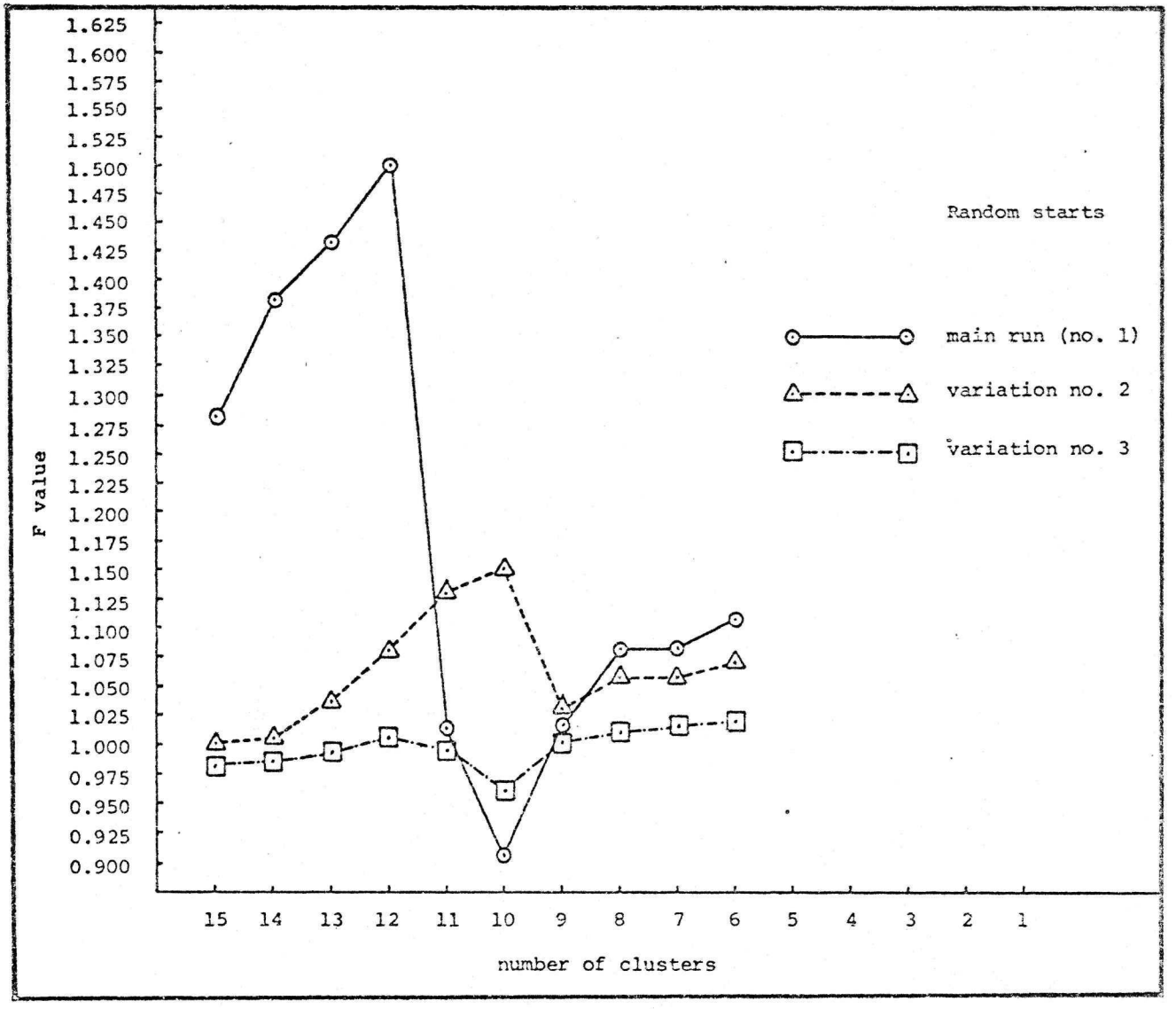


Fig. 6. F value variation with cluster number.

are given in Table 4. It is interesting to note in Fig. 6 that the F value graphs for the 3 random starts show the closest agreement at the 9 cluster level, while they are widely separated at the 10 cluster level. The trap sites were then mapped according to the spatial distribution of the clusters (Fig. 7).

The nine clusters were considered to satisfy the requirements of definable habitats. It is evident from Fig. 7 and Table 4 that the burn contains fewer distinct habitats than the control. The burn lacks the lichen and moss dominated habitats, while the control lacks the grass dominated habitat.

Table 5 gives the results of a X^2 test of small mammal distributions in comparison to that of habitat type. M. pennsylvanicus showed a positive association with the most productive habitat in the burn in 1973 while C. rutilus did not. Habitat type 4 was numerically the most productive in the control, but it was represented by only two trap sites. Habitat 6 was second in productivity and represented by 48 trap sites. C. rutilus shows a positive association with this habitat in both years. In the control in 1973 M. pennsylvanicus showed a positive association for habitat 3 which was avoided by C. rutilus in both years. When the two populations became roughly equal at much lower levels

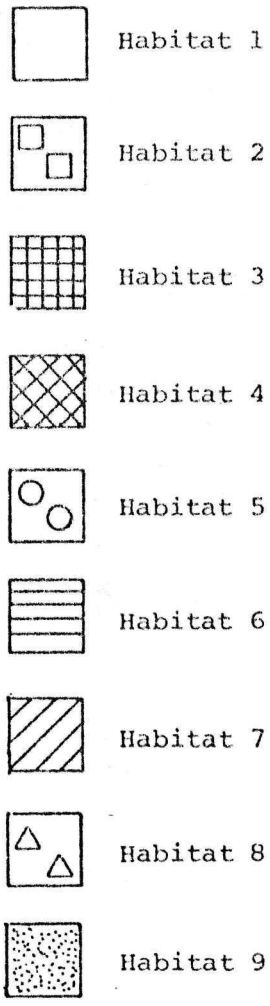
TABLE 4

Habitat summary chart

Cluster	Floral composition	Cluster cover means (%)	Occurrence (%)		Productivity (g/m^2)	
			Burn	Control	Burn	Control
1	*Ledum groenlandicum*	5.4	50.8	34.8	67.4	77.9
	Equisetum scirpoides	2.4				
	Epilobium angustifolium	0.3				
2	*Hylacomium splendens*	26.0	*	10.8	*	69.5
	Pyrola secunda	1.1				
	Pyrola grandiflora	0.9				
3	*Vaccinium uliginosum*	22.7	12.0	12.4	82.8	100.0
	Vaccinium vitis-idaea	4.9				
	Picea mariana	1.2				
4	*Carex lugens*	51.4	10.4	0.8	175.5	242.9
	Salix arbusculoides	6.4				
	Rubus chamaemorus	0.5				
5	*Calamagrostis canadensis*	51.7	4.4	*	76.4	*
	Salix glauca	20.9				
	Rosa acicularis	4.2				
	Epilobium angustifolium	1.7				
6	*Aulacomium nitens*	35.8	*	19.2	*	177.8
	Arctostaphylos rubra	6.9				
	Equisetum scirpoides	3.0				
7	*Alnus crispa*	31.0	1.6	4.4	96.3	74.6
	Pyrola grandiflora	16.7				
	Picea mariana	1.3				
8	*Cladonia rangiferina*	22.2	*	10.8	*	93.0
	Vaccinium vitis-idaea	7.2				
	Empetrum nigrum	3.5				
	Ledum palustre	0.6				
9	*Carex lugens*	23.9	20.8	6.8	117.1	155.5
	Polytrichum juniperinum	2.9				
	Tomenhypnum nitens	2.4				
	Potentilla fruticosa	1.2				
	Eriophorum spissum	1.2				
	Betula glandulosa	1.1				

* Habitat does not occur on the plot.

Fig. 7. Habitat maps of burn and control grids.



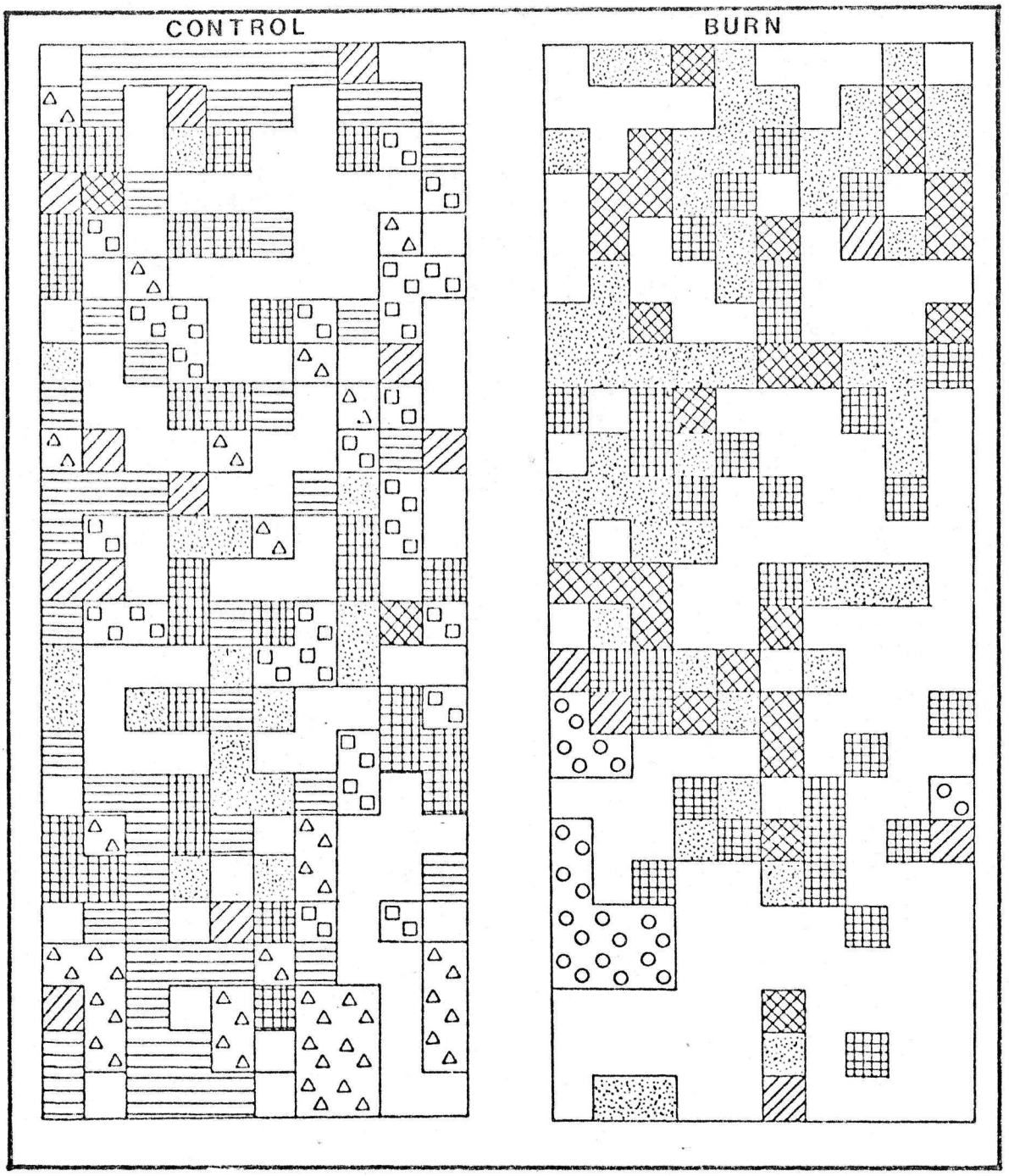

CONTROL
BURN

TABLE 5

Habitat-vole associations

	Control								Σ captures	Burn						Σ captures
Habitat type	1	2	3	4	6	7	8	9		1	3	4	5	7	9	
No. of trapsites in each habitat	87	27	31	2	48	11	27	17		127	30	26	11	4	52	
Productivity (g/m^2)	77.9	69.5	100.0	242.9	177.8	74.6	93.0	155.5		67.4	82.8	175.5	76.4	96.3	117.1	
Small mammal species:																
Clethrionomys rutilus: 1973	354 ⊕	89	59 ⊖	1	240 ⊕	36	91	29 ⊖	899	69	11	13	18 ⊕	6 ⊕	24	141
1974	102	27	27 ⊖	3	95 ⊕	11	25	16	306	**						
Microtus pennsylvanicus: 1973	11	2	9 ⊕	0	5	0	6 ⊕	3	36	133 ⊖	46	69 ⊕	13	0 ⊖	79	340
1974	38 ⊖	10	26	3	42 ⊕	0 ⊖	33	7	159	**						
Microtus xanthognathus: 1973	69 ⊕*	17	10 ⊖	4 ⊕	23	13 ⊕	13 ⊖	9	158	**						
1974	76 ⊕	15	13 ⊖*	2	40	9	8	7	170	**						

⊕ = positive association
⊖ = negative association
) significant at p 0.05

⊖* = p 0,10

** = insufficient sample size

in 1974, both rodents showed a positive association with the most productive habitat.

M. xanthognathus was the only small mammal to show a preference for habitat 1 over both years in the control. It also avoided habitat 3 over both years as did C. rutilus. This habitat is the only one to which M. pennsylvanicus showed a positive association in 1973.

DISCUSSION

Growing conditions in the burn were sufficiently favorable to allow an increased production of most ground flora over that observed in the control. Vaccinium uliginosum was the most frequent plant encountered in both areas and occurred at very close cover values. This suggests a rapid return in the burn from rootstocks which had a preburn abundance similar to that in the control. V. uliginosum responded to fire in the burn with a greatly increased sprouting of rooted stems and production of vegetative and reproductive parts.

The lack of an insulating moss and lichen cover in the burn permitted mineral soil to thaw to a greater depth and released previously frozen ground to exploration by plant roots. Periodic removal of this slowly decaying moss mat may be an important process in boreal ecosystems, especially those situated on permafrost. Rowe and Scotter (1973) found that forest growth under conditions of heavy moss cover and shallow thaw depth became much slower compared to that observed in more southern regions. These periods of accelerated growth may also have importance in maintaining the vigour of perennial rootstocks and thus provide benefit for

the plant long after the immediate effects of fire have passed

The ragged plateaus of dry weights over the summer (Fig. 4) may be induced by variable weather. Non-vascular production in the control accounted for a major portion of the net primary production in that plot. Reader and Stewart (1971) state a value of 55.4g/m^2 for total non-vascular production, and 5.4 g/m^2 for Aulacomnium palustre in southeastern Manitoba, compared to the 72.9 g/m^2 total and 58.3 g/m^2 value for Aulacomnium nitens found in this study. These authors report a total net vascular aerial production of 316.4 g/m^2 which is far in excess of the 157.1 g/m^2 and 134.9 g/m^2 found for the burn and control, respectively. Their study area was not located on permafrost, however, and the growing season was considerably longer.

The similarity of the burn and control in the composition of ground flora suggests that the post-fire succession flora in this area is not distinct from that of older sites. Lutz (1956) similarly noted that post-burn flora in Alaska consisted mainly of previously occurring species. Conversely, the floral types observed in this study may actually be an early successional state that is not allowed to progress to maturity due to high fire frequency, a view held by Vireck (1973) for taiga in Alaska. Reid (1974) inves-

tigated boreal growth processes in northern Canada and concluded that as moss growth accumulated, forests became thinner until a sparsely treed raised bog resulted. This process has also been described by Heinselman (1970) for peatlands in Minnesota. Forest growth may thus be maintained in far northern regions by the removal of the moss mat by fire before the process of peatland formation can begin.

Habitat definition by cluster analysis provides one method by which subtle plant associations can be revealed. This is especially important in boreal areas due to the heterogeneity of the ground flora. Whether the groupings which result have any meaning to an animal population in terms of actual habitat is dependent on whether the parameters used in the analysis actually affect the distribution of that population. This technique is also sensitive to the amount of information used in the analysis since different associations will be formed as more parameters are measured.

These clusters do not represent habitats in any limiting sense; rather they are subunits of the animal's entire habitat range. All species in this study were captured in all habitats, however the distribution of captures throughout these habitats was not uniform. This can be the result of habitat preferences exercised on the part of the animal, or external factors such as behavioural interaction with

other species.

The population peaks of C. rutilus and M. pennsylvanicus in 1973 occurred in the control and burn, respectively. C. rutilus maintained a small population in the burn; however, M. pennsylvanicus was essentially absent in the control. The following year, however, both coexisted at roughly equal numbers in the control, but were rare in the burn. M. pennsylvanicus is usually associated with grasslands, and where it was found with Clethrionomys gapperi in more southern areas, habitat segregation into grassland and woodland occurred (Grant and Morris 1971). Coexistence of these two species was recorded by Iverson and Turner (1972). They found that C. gapperi moved into grassland in winter and returned to woodland with the onset of breeding in M. pennsylvanicus in spring. In this study, C. rutilus and M. pennsylvanicus coexisted in woodland at low population levels. At peak population levels M. pennsylvanicus was rare in woodland, but abundant in a recent burn.

Both C. rutilus and M. pennsylvanicus in 1973 showed a positive association with the most productive habitat in the area in which they were dominant, and a null or negative association with the most productive habitat in the area in which they were rare. In 1974 both species were positively associated with the most productive habitat in the control.

This suggests that each is more competitive in the area in which their population peaks occurred, but coexist at lower density. Getz (1970) found that M. pennsylvanicus occupies the optimum habitat at population lows and disperses to less favorable areas as the population increases. In this case while the burn supported a peak population it was avoided at low levels, indicating that it is not a favorable habitat if older sites are available.

The sex ratio differences shown in Fig. 5 suggest a behavioral difference between sexes to trapping. Recent work has shown that several demographic and behavioral characteristics of vole populations change over the course of a fluctuation in abundance (Krebs 1970, Krebs et al. 1973, and Gaines and Krebs 1970). Myers and Krebs (1974) observed in Microtus that dispersal increased as population levels increased with females the most common dispersers at that time. More female C. rutilus were captured in the burn in July of 1973; however, this reversed in August to that observed in the control where males predominated. Since the population in the control in July was increasing, dispersal of females into the burn may be responsible for their temporary predominance at that time.

CONCLUSION

In order to discover the nature of fire recovery in a far northern area, a recent burn (1969) and an old burn (about 1849) were compared in terms of plant and animal communities and productivity. The vascular floral composition of each area was found to be similar, although the new burn lacked cryptogams. Vascular production was higher in the new burn although total net primary productivity was higher in the old burn due to a large contribution from the non-vascular component.

Microtus pennsylvanicus, M. xanthognathus and Clethrionomys rutilus were captured in both areas. M. pennsylvanicus and C. rutilus were at peak population levels in 1973, but these peaks occurred separarely in the new and old burns respectively. When populations fell the following year both rodents were found at nearly equal numbers in the old burn, but were absent from the recent burn. Habitat studies by clustering analysis revealed nine distinct floral associations; of which eight occurred in the old burn and five in the new burn. When small mammal distributions were compared to habitat distribution it was found that each rodent species

showed a positive association with the most productive habitat in the area in which it was dominant in 1973, but avoided this habitat in the area in which it was rare. In 1974, however, both M. pennsylvanicus and C. rutilus selected the most productive habitat on the old burn when their population levels dropped. This suggested that at high population levels, C. rutilus was the more competitive species in the old burn, while M. pennsylvanicus was able to take advantage of the habitats available in the new burn. Optimum habitat for these species remains in the old burn however, since this was the area selected when population levels dropped in 1974.

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